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SHORTER ARTICLES AND DISCUSSION

COLLINS'S REMARKS ON THE VIGOR OF FIRST GENERATION HYBRIDS

IN a review of the theories regarding hybrid vigor Collins[1] has attempted to show that the two objections which were long upheld as precluding the possibility of dominance accounting for heterosis were without foundation. The suppression of deleterious factors, he considers, is adequate to account for the observed facts without considering the phenomenon of linkage.

The two objections which were raised against the hypothesis of dominance as a factor in hybrid vigor before the importance of linkage became generally known are as follows: (1) Dominance of independent factors would give an asymmetrical distribution to the progeny populations of those individuals which show an increase in growth when crossed. (2) Free assortment would make possible a recombination of all the dominant favorable growth factors into a homozygous fixed race which would not be reduced by inbreeding. Neither of these objections holds when linkage is taken into consideration. Collins believes that they also do not apply when linkage is left out of consideration.

Collins shows numerically and graphically that with a large number of factors involved the skew curve of the theoretical distribution of independent dominant factors approaches the type of the normal curve. He points out that, with characters dependent upon a large number of factors, only populations with larger numbers than have been dealt with statistically would exhibit any noticeable tendency toward skewness. This is a good point well brought out which previously had been neglected. But this would apply only to progenies which have a restricted range in comparison with their parental populations. In those cases where the range of the segregating generations with small numbers nearly equals the combined range of the original races as exhibited by the characters which show heterosis the number of main factors which govern the expression of this particular character can not be large. Therefore, if it were merely a matter of dominance without linkage, such distributions would be expected to show right-hand skewness. But they do not consistently do so.

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[1] Dominance and the vigor of first generation hybrids. AMER. NAT., 55: 116–133, 1921.

In regard to the second objection, that of recombination of all favorable factors, Collins has given a large number of figures to show what was already well known, that with a large number of factors the chances for recombination are remote with the small progenies grown in experimental plots. It was not intended to maintain that pedigree cultures were adequate to show that such a recombination could not be made. The point in mind, if not clearly expressed, was that natural selection in isolated populations of cultivated plants had not brought about any noticeable approach to stability. In the hills of New England maize has been grown for long periods of time in isolated fields. Some varieties have probably been grown for at least fifty years without admixture. Yet these varieties when self-fertilized show as rapid a reduction in growth as other varieties which are lately the product of extensive hybridization.

There is an enormous difference in the possibilities for immediate recombination with and without linkage. To illustrate: with twenty independent factors the chance for the bringing together of all dominants in a homozygous state in one generation is theoretically one in 4^{20}. With the same twenty factors distributed by twos in ten different chromosomes, each being separated by ten units of crossing-over, the chance for recombination is theoretically one in 20^{20}. This is a difference in total numbers so vast as to be almost inconceivable. Working over long periods of time, linkage may not be a hindrance to recombination, as factors once brought together tend to stay together as firmly as they once resisted separation. Many cross-fertilized species in the wild whose age is measured in geological periods rather than years are stable. But cultivated forms even when isolated for a considerable time show no noticeable approach toward this condition. It seems reasonable to suppose that the arrangement of factors in the chromosomes has something to do with this state of affairs. Therefore, until the chromosome theory of heredity was developed, there was considerable plausibility to the older view that something besides mere dominance was responsible for heterosis.

Even so, I am perfectly willing to admit that there is no clear way of deciding the argument as to whether or not the old objections were valid. But how important is it now to make this decision? Linkage is a fact and must be taken into consideration. True, the evidence in support of the chromosome hypothesis from maize is not extensive. But hybrid vigor is a widespread phenomenon shown by many organisms. The dominance hypothesis applies to *Drosophila* as well as to maize.

This failure to look outside of the corn field has led Collins to make certain statements to which I must take strong objection. He is inclined to believe that the suppression of deleterious factors is all that is involved in the vigor derived from crossing. This may be true for *Drosophila,* but there are many cases of wild species of both animals and plants as well as of naturally self-fertilized varieties of cultivated plants which show an unmistakable increase in growth after crossing. Take Naudin's *Datura* crosses which doubled in height, Kölreuter's *Nicotiana* hybrids which astonished their producer, the hybrid walnuts, both natural and artificial, and Gerschler's fish hybrids, to name a few notable illustrations. Collins himself has given us several good illustrations of remarkable vigor shown by hybrids of many varieties of maize from different parts of the world. Here it is clearly not a matter of suppressing deleterious characters. The parental types are normal, vigorous and perfectly capable of maintaining themselves in their own way. But crossing brings about a new combination of hereditary qualities. By utilizing the best from both parents the hybrid is able to obtain a surpassing development. As long as variation exists different individuals will have unlike germinal potentialities. Crossing tends to bring these different possibilities together. Dominance enables the offspring to take advantage of the more favorable factors. This is as true of domesticated races as it is for wild species.

Furthermore, there is abundant evidence that many factors are without effect unless working in consort. In plants, colors of various parts, and in animals, coat patterns, are conspicuous examples of this complementary action. These characters are possibly of no importance in growth, yet they illustrate a state of affairs which is probably of real significance. Crossing makes it possible to assemble the component parts.

As Collins says, to consider hybrid vigor as the suppression of deleterious heredity as compared to the bringing together of a greater number of favorable growth factors is, to a certain extent, merely a different way of looking at the same thing. But it puts the emphasis on the wrong side and is wholly inadequate to account for all the manifestations of hybrid vigor. It would be unnecessary to discuss this were it not for the fact that his way of looking at the matter leads him to think that there is no essential distinction between the Darwinian view of inbreeding as a process leading toward extinction and the more recent conception that the results of this system of mating depend upon the inheritance received. Collins says:

> Many of the older writers on heredity have held that inbreeding is a cause of degeneration. In avoiding ambiguous words "cause" is one of the first that must go. If forced to define their position this school would probably be content with the statement that degeneration is a necessary consequence of inbreeding, the intermediate step or nature of the process being unknown. Is this conception really at variance with the idea that degeneration results from the increased number of unfavorable recessive characters brought into expression by increased homozygosity? Does not this conception rather amplify the older, general and indefinite position by explaining how degeneration may be brought about? (P. 124.)

Leaving aside all question of definition of terms, let us consider the results of the two views when applied in practise. To say that abnormal and undesirable individuals appear after close mating is very different from supposing that such forms have their origin in the system of mating. Whether or not this is stating the matter fairly, breeding practises have been in accord with the latter view. As a result of inbreeding we now know that aberrant individuals bordering on the teratological often come to light. Along with these types which are truly degenerate in any sense of the term (but inbreeding has nothing to do with their origin) there are perfectly normal individuals which suffer in comparison with their more heterozygous parents in that they are only slower in growth, are not so resistant to unfavorable conditions and are not so productive. Inbreeding is solely a process of sorting out. Some bad material is brought to view which can be discarded. But along with this there is all the good material that was in the stock, and this can be used to rebuild a better breed than existed at the start. Before the era of Mendelism there was little conception that it was the stock that was at fault and not the system of mating. Even though it was the appearance of abnormal and bizarre forms which gave the bad name to inbreeding in the past, the less vigorous offspring frequently resulting from inbreeding, although healthy, were also considered to be valueless for further propagation and were quickly disposed of.

This is still the belief and practise of live-stock breeders. Those who do not know the principles involved think that inbreeding has permanently injured the families with such weakened individuals. Equipped with the results of two decades of genetic investigation, we can say, "No! this is not so. *Nothing has been lost.* These less vigorous inbred individuals of no apparent worth have potentially great value." A widespread reception of this idea has possibilities of great practical outcome. Not to see clearly the important distinction which there is here between the present and former views is not to appreciate the real progress which the combined genetic research of twenty years has made along this line.

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AN APPARENT CASE OF SOMATIC SEGREGATION INVOLVING TWO LINKED FACTORS[1]

Somatic segregation as an ordinary occurrence, and especially as a source of definite progeny ratios in subsequent sexual reproduction, seems highly improbable. The evidence connecting normal segregation and recombination with meiosis and fertilization is too strong. As a matter of occasional mitotic abnormality in heterozygous material, however, the question of somatic segregation is still open.

Any "bud sport" involving apparently simultaneous change of two or more non-allelomorphic factors is therefore of special interest, since the probability of its occurrence through two nearly simultaneous factor or point mutations seems very remote. Either deficiency mutation, which seems to mean (Bridges, 1917) the loss of a normally present portion of a chromosome, or the development or resolution of a condition of "duplication" (such as vermilion-sable duplication in *Drosophila melanogaster;* Bridges, 1919, p. 646) might produce the effect in question. So, also, might a process properly described as "somatic segregation," in which at some mitosis one daughter

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[1] Paper No. 60, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.